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THE MENDELIAN NOTATION AS A DESCRIPTION OF PHYSIOLOGICAL FACTS

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As I understand Mendelism[1] it is a concept pure and simple. One crosses various animals or plants and records the results. With the duplication of experiments under comparatively constant environments these results recur with sufficient definiteness to justify the use of a notation in which theoretical genes located in the germ cells replace actual somatic characters found by experiment. This is done wholly to simplify the description of the experimental results. If one finds that the expression $DR \times DR = 1DD + 2DR + 1RR$ adequately represents the facts in numerous breeding experiments, he is then able to use the knowledge and the expression in predicting the results of other similar experiments. Mendelism is therefore just such a conceptual notation as is used in algebra or in chemistry. No one objects to expressing a circle as $x^2 + y^2 = r^2$. No one objects to saying that $BaCl_2 + H_2SO_4 = BaSO_4 + 2HCl$. No one should object to saying that $DR + RR = 1DR + 1RR$. We push things into the germ cells as we place the dollars in the magician's hat. Hocuspocus! They disappear! Presto! Out they come again! If we have marked our money we may find that that which appears from the magician's false-bottomed hat is not the same as that which we put in. But it looks the same and is good coin of the realm. We have a good right therefore to poke our characters into the germ cell and to pull them out again if by so doing we can develop—not a true conception of the mechanism of heredity—but a scheme that aids in describing an inheritance. We may do this even as we may use algebraical and chemical notations, if we remember that $x^2 + y^2$ does not give us a circle, that a chemical equation does not represent a true reaction or prove the atomic theory, that we have not pulled something new and astonishing out of the germ cell, that a unit factor represents an idea and not a reality, though it must have a broad basis of reality if it is to describe a series of genetic facts.

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[1] I do not speak here of the new biological facts discovered by Mendel or by his followers. Facts are always facts. Alternative inheritance and character recombinations were important facts, but I think no one will deny that the greatest value of Mendel's facts arose from the mathematical treatment he gave them. This mathematical notation remains conceptual just as does the chemical formula, but it must have as much basis of fact as there are pertinent facts extant.

The facts of heredity that one describes in the higher organisms are the actual somatic characters, variable things indeed, but still things concrete. Their potentialities are transmitted to a new generation by the germ cells. We know nothing of this germ cell beyond a few superficial facts, but since a short description of the breeding facts demands a unit of description, the term unit factor has been coined. As I hope to show, a factor,[2] not being a biological reality but a descriptive term, must be fixed and unchangeable. If it were otherwise it would present no points of advantage in describing varying characters. The only obvious reason for poking it into the germ cell is to distinguish thus the actual parent (the cell) from the putative parent (the carrier).

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[2] I hope this statement is not confusing. The term factor represents in a way a biological reality of whose nature we are ignorant just as a structural molecular formula represents fundamentally a reality, yet both as they are used mathematically are concepts.

If we forget ourselves and begin to speak of unit factors as particles, only a confusion follows similar to that caused by Nägeli, Spencer and Weismann. Nothing is gained and even facts are obscured.

THE SCOPE OF MENDELISM

How far may we carry this conceptual notation? My answer is: just as far as the notation interprets the facts of breeding and is helpful. Interest in the scope of Mendelism is now focused on two phases, complete and partial coupling and the interpretation of so-called size characters. Complete coupling in the transmission of characters apparently non-related has been shown in a large number of cases. Perhaps those best worked out in animals are the sex-coupled or sex-limited characters observed by Morgan in *Drosophila.* In plants, cases observed by Emerson and by Bateson and his coworkers are equally clear. Emerson has shown beyond a reasonable doubt that the characters he describes are independent of each other, and can not be represented by one factor. Bateson has recently corroborated the observation on other characters. Besides this phenomenon, Bateson has discovered partially coupled characters. All three of these writers, have subsidiary hypotheses to account for their facts. Bateson, when discussing perfect couplings, merely says that the characters come out in F_2 coupled in the way they went in in the grandparents, which naturally is only a restatement of the facts. Morgan and Emerson deal in pictures of carrying bodies. Both of their theories fit their own facts as they necessarily would. Emerson and, I may say, myself believe Morgan's theory incompatible with that of Emerson. Morgan believes his theory adequate for both cases. Without discussing the merits of these particular hypotheses I think it is agreed that some characters do go into the F_1 generation and come out from it together that are in other cases independent. The importance of the phenomenon is greater than the theory at present.

It has been questioned whether one has the right to continue to couple characters in large numbers to interpret facts, because by proper coupling one may interpret almost any fact, and place himself in a logically unassailable position. But this is no reason for not coupling factors as much as one pleases if it is helpful and if all of the facts fit. *A propos* of this statement I might say that I have recently remade the historical old cross first made by Kölreuter in 1760, *Nicotiana rustica* × *Nicotiana paniculata*. These species differ in many details—habit of growth, size, shape and hairiness of leaf, inflorescence, and size and shape of flower and fruit. Both of the parent species have been reproduced exactly from a partially fertile F_1 in a total number of less than 200 F_2 plants. One may formulate an hypothesis of selective elimination of gametes combined with selective fertilization that helps to describe the facts, but unless large numbers of factors are coupled together I believe it to be impossible to account for all the facts by the usual Mendelian notation.

Before leaving this subject it might be mentioned that Bateson's theory, originated to account for partial coupling, keeps the idea of factors segregating from their absence, but instead of A and a being formed in equal quantities as in "regular" Mendelian notation, they are to be formed in series represented by the scheme $n-1AB : 1AB : 1aB : n-1ab$. I do not believe one should hasten to accept this description, although Bateson's F_2 generation facts certainly fit and have been recently supported by Baur. My reason for making this statement is that as yet Bateson's F_3 facts do not fit the theory. Some of them would even make necessary two or more different kinds of factorial distribution in the same plant varieties. On this score the helpfulness of our notation[3] is impaired and this is the only excuse for its existence. Furthermore, while it has not been proved that the phenomenon we call segregation occurs at the reduction division, the presumption is in favor of that view. The work of Webber, Correns, Lock, Emerson and myself on *Xenia* in maize indicates that segregation does not take place immediately after reduction, while the work of the Marchals on regeneration in mosses indicates that it does not take place before reduction.

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[3] Here is a good illustration of the Mendelian notation as a concept. Supposing the gametic distribution $n-1AB : 1Ab : 1aB : n-1ab$ were to fit all the facts in the case, then no one could object to its use. If it were to be demonstrated that segregation occurred at the reduction division, however, the scheme no longer fits the facts and must be abandoned.

Now to turn to the kinds of variation that may be described by the Mendelian notation. Owing to its youth, we can all remember how we wondered, as each new case came up, whether Mendelian phraseology would fit. Since qualitative characters were the ones that could be divided into definite categories they were the ones attacked. One by one they were analyzed. The phraseology did fit. Qualitative characters however form a very small proportion of the characters in animals and plants. The numerous characters are the quantitative, the size characters. If Mendel's law is to be worth anything as a generality, therefore, it must describe the inheritance of these characters.

To some of us Mendel's law from the first seemed destined to be a notation generally useful in describing inheritance in sexual reproduction. This conclusion was indicated by the simple fact that Mendel's law described many cases in both the animal and the vegetable kingdom. It was inconceivable that this should be the result of coincidence. It was therefore still more inconceivable that only a small portion of the facts in each kingdom should come under the scope of Mendelism.

A basis for the inclusion of quantitative characters was obtained when Nilsson-Ehle and the writer showed that certain qualitative characters gave ratios of 15:1, 63:1, etc., in the F_2 generation, and in other ways behaved so that they might be described only by assuming more than one independent gametic factor as the germ cell representative of the character, if the orthodox idea of segregation were retained. From these phenomena it was immediately seen that where dominance is absent and such multiple factors are assumed, size characters can be interpreted as coming under the Mendelian law. When dominance is complete the mathematical representation of an F_2 generation is $(3/4 + 1/4)^n$ where n represents the number of factorial differences involved; as the manifestation of dominance becomes less this formula approaches the type $(1/2 + 1/2)^{2n}$. The difference between the heredity of qualitative characters and quantitative characters is therefore only one of degree, for there is absence of dominance in cases of simple monohybrid qualitative characters and there is presence of multiple factors in cases of qualitative characters showing dominance. But it is manifestly absurd to expect size characters to appear in natural groups as do many qualitative characters. The marked effect of environment and our ignorance of the exact effect to attribute to each factor precludes it. One can determine whether size inheritance compares with the inheritance of qualitative characters only by the use of arbitrary biometrical methods. In theory, homozygotes with size differences when crossed should give an intermediate F_1 of low variability and an F_2 of high variability. Various F_3 populations should differ in their mean and in their variability. The difference in the variability of F_2 over F_1 should decrease as the heterozygosity of the parents increases. Sometimes parents of the same size should differ in the factors they contain and the F_2 generation should contain individuals smaller and individuals larger than either of the parents. Each of these requirements has been satisfied by experiment. East and East and Hayes have tested it for number of rows per cob, height of plant, length of ear and size of seed in maize, Shull for number of rows in maize, Emerson for fruit sizes in maize, beans and gourds, Tammes for various characters in flax species, Tschermak for time of blooming in beans, Hayes for number of leaves in tobacco, Belling for certain characters in beans, Phillips for body size in ducks, MacDowell for body size in rabbits. In these investigations every test possible for the theory has been satisfied. No criticism could be made except that certain of the characters used varied considerably in the mother varieties and therefore were presumably not homozygous for all character factors. This criticism is apparently answered by a recent investigation of the writer's, as yet unpublished, where two species, *Nicotiana forgetiana* and *Nicotiana alata grandiflora* were crossed. As seen by the table, the corolla length is very slightly variable in either species, nor is it affected to any extent by environment, yet each species was absolutely reproduced by recombination in the F_2 generation.

TABLE I

FREQUENCY DISTRIBUTIONS FOR LENGTH OF COROLLA IN A CROSS BETWEEN *Nicotiana forgetiana* (314) AND *N. alata grandiflora* (321).

Designation	Class Centers in Millimeters														
	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90
314	9	133	28												
321										1	19	50	56	32	9
(314 × 321) F_1				3	30	58	20								
(314 × 321) F_2		5	27	79	136	125	132	102	105	64	30	15	6	2	

Coefficients of variation are: 314 = 8.86 ± .33 per cent.; 321 = 6.82 ± .25 per cent.; (314 × 321) F_1 = 8.28 ± .38 per cent.; (314 × 321) F_2 = 22.57 ± 39 per cent.

I do not believe that biologists have sufficient facts as yet to warrant any concrete meaning being given to their notation as regards germ-cell structure, but I do maintain that the Mendelian notation satisfies the facts of size inheritance as well as it satisfies the facts of qualitative inheritance. As a description, it goes the whole way. If qualitative inheritance is Mendelian, quantitative inheritance is Mendelian; if quantitative inheritance is not thus described, qualitative inheritance is described not a whit better.

All writers do not agree with this statement; nevertheless, speaking for myself only, I believe it to be beyond question. Castle (AMER. NAT., 46: p. 361) says:

> It is quite possible that we are stretching Mendelism too far in

> making it cover such cases. Dominance is clearly absent and the only fact suggesting segregation is the increased variability of the second as compared with the first hybrid generation. This fact however may be accounted for on other grounds than the existence of multiple units of unvarying power.
>
> If size differences are due to quantitative variations in special materials within the cell, it is not necessary to suppose that these materials are localized in chunks of uniform and unvarying size, or that they occur in any particular number of chunks, yet the genotype hypothesis involves one or both of these assumptions. Both are unnecessary. Variability would result whether the growth-inducing substances were localized or not, provided only that they were not homogeneous in distribution throughout the cell. Crossing would increase variability beyond the first generation of offspring because it would increase the heterogeneity of the zygote in special substances (though not its total content of such substances) and this heterogeneity of structure would lead to greater quantitative variation in such materials among the gametes arising from the heterozygote. Thus greater variability would appear in the second hybrid generation.

I can not agree with this statement as I understand it, though this disagreement may be due to my own limitations. We do not stretch Mendelism and we do not make it cover such cases. The facts of breeding have been obtained and the Mendelian notation expresses them. That is all that it is necessary to claim. It is not precisely true, however, to say that increased variability in the second hybrid generation is the only fact to be expressed. It is of paramount importance that various F_2 individuals giving F_3 populations differing in mean and in variability, should be included in the Mendelian description. They are included.

Again, Castle states that the genotype conception assumes the localization of the hypothetical factors either in chunks of uniform and unvarying size, or that they are carried by a particular number of chunks. I am unaware of any such assumptions. It is true that some such picture has been suggested as a diagram helpful to the imagination in its conception of the scheme as a mechanical process, but this is purely and simply a diagram. The real matter under discussion is that the breeding facts are adequately described in a notation essentially Mendelian.

Of course Castle's scheme of expressing the facts by heterogeneity in the germ cell might serve. He produces increased variability in the second hybrid generation by greater differentiation among the gametes arising from the heterozygote. But one can also describe inheritance of qualitative characters in the same way, and one gains no system by it. It is a return to the type of expression used by Nägeli, Naudin and De Lage in pre-Mendelian days. It is simply a trans-nomination possessing no advantages.

Before leaving this phase of the subject, I must speak of Davis's recent fine paper (Amer. Nat., 46: p. 415) on his crosses between *Œnothera biennis* and *Œnothera grandiflora*. As I have had the advantage of seeing his cultures many times in the past two years, I am in a fair position to draw my own conclusions as to the meaning of his data. In regard to his F_2 generation from the hybrid plant marked 10.30 L *b* he says:

> 1. In the immensely greater diversity exhibited by the F_2 generation over that of the F_1 is clearly shown a differentiation of the germ plasm expressed by the appearance in the F_2 plants of definite tendencies in directions toward the two parents of the cross. This seems to the writer the essential principle of Mendelism and does not necessarily involve the acceptance of the doctrine of unit characters and their segregation in either modified or unmodified form.
>
> 2. Certain characters of the parent species have appeared in the F_2 segregates in apparently pure condition, but the very large range of intermediate conditions indicates that factors governing the form and measurements of organs (if present at all) must in some cases be concerned with characters so numerous and so small that they can not be separated from the possible range of fluctuating variations. If this is true such characters seem beyond the possibility of isolation and analysis and the unit character hypothesis for these cases has little more than a theoretical interest.
>
> 3. Both cultures certainly showed marked progressive advance in the range of flower size, the largest flowers having petals somewhat more than 1 cm. longer than those of the *grandiflora* parent. There was a similar advance in the size of the leaves and the extent of their crinkling. These progressive advances would seem to demand on the unit character hypothesis either the modification of the old or the creation of new factors.
>
> 4. The absence of classes among the F_2 hybrids (except for the

dwarfs) further works against the unit character hypothesis as of practical value in the analysis of a hybrid generation of this character. It should be remembered, however, that there were in this cross no sharply contrasted distinctions of color, anthocyan (stem) coloration proving most unsatisfactory for the purpose of a genetical study.

These four paragraphs are practically a résumé of Davis's genetic facts: I take exception only to some of the implied conclusions. It is quite evident that Dr. Davis believes that many breeding facts are expressed in shorthand by the Mendelian notation. His statements, however, imply a feeling of loss of caste or something of the kind if he makes definite use of Mendelian phraseology. His F_2 generation was exactly what would be expected when several Mendelian units without dominance segregate and recombine. The advance in size of corolla was predicted by me in 1910 (AMER. NAT., 44: p. 81) as a direct consequence of size inheritance. It has since been demonstrated by Tschermak for time of blossoming of beans and clearly analyzed by Hayes for number of tobacco leaves. It demands neither modification of old nor the creation of new factors. It occurs whenever *AABB* (size factors) is crossed with *CCDD,* and each factor is allelomorphic to its own absence, to use the ordinary phraseology.

As to the difficulty of precise analysis into factors, I agree with Dr. Davis, but that there is no advantage in showing that this behavior is described in typical Mendelian terms I can not admit. One holds the same practical advantage here—though the case is complex—that one holds in all Mendelian inheritance. He knows that somatic appearance is not the criterion of breeding capacity, but that it is determined in some way by gametic constitution, although no germ cell architecture is presupposed. He knows that recombination of some kind of factors occurs and has some idea of the number of progeny to be grown to obtain the desired combination. In other words, the blend in F_1 does not indicate complete loss of extremes.

Mendel's Law and Galton's Law

The above statement leads into a discussion of Mendel's law of heredity as compared with Galton's law, for in itself it is almost a statement of the difference. As Bateson was the first to emphasize, organisms inherit from parental germ cells only, therefore a law of ancestral heredity is a fallacy and a misnomer. The simple illustration that of two individuals alike in appearance one is homozygous for a character and the other heterozygous for the same character, shows the superficial reasoning that leads to the correlation coefficient as a measure of heredity. Parental and filial populations may show correlation, but that is only a matter of averages and not a measure of the inheritance.

Professor Castle has recently disclosed the probable Mendelian basis for Galton's data on coat color of Bassett hounds by showing the inheritance of tricolor coat in guinea-pigs, yet he makes the surprising statement that "as regards height, however, and other size characters, Galton's law is quite as good a basis for predicting the result of particular matings as is Mendel's." The arch priest of biometry, Karl Pearson, does not claim that Galton's law can predict the result of individual matings. Similarly, Mendel's law predicts only by averages. It says that where DR meets DR, there will be on the average $1DD:2DR:1RR$ produced. Where the classes are larger the prediction in increasingly complicated. But the prediction is as good for size characters as for qualitative characters of the same complication. And there are such qualitative complications, as is manifest by Castle's formula of $AACCUUIIYYBBBrBrEE$ for a wild rabbit's coat color. The difference between Galton's law and Mendel's law is that the true criterion of the germ plasm of any individual is its breeding *power* and not the somatic appearance of its back ancestry. This is as true of size characters as of any other characters.

The Genotype Conception of Heredity

Expressed in Johannsen's words, the basis of the modern conception of heredity is: "Personal qualities are the *reactions of the gametes joining to form a zygote;* but the nature of the gametes is not determined by the personal qualities of the parents or ancestors in question." The quotation expresses well the idea that I have just tried to convey, and from it one sees plainly that it is the correlation that necessarily appears to a greater or less extent between the somatic qualities of two generations when they exist in large numbers that gave the basis for Galton's superficial law.

This quotation is Johannsen's slogan for the genotype conception of heredity. As there stated, it is merely a generalized expression of the essential features of the Mendelian notation. Johannsen, therefore, was the first to admit the broadness of its scope. In his exposition of his position, however, he adds two subsidiary propositions that we will now discuss; the first is the perennial question of the possibility of the inheritance of acquired characters, the second is a question which from its illusiveness is likely to take on a perennial habit—that of the relative constancy of unit characters.

In regard to the first question I must be content here with a mere general statement. Like Osborn I would emphasize the possibly delusively static condition of organisms when tested during the infinitesimal time usually devoted to experiment. The inheritance of acquirements in some subtle way unknown to us may have been of immense importance in evolution. On the other hand, some sort of an orthogenesis may account for all the facts without the inheritance of acquired characters. It scarcely seems possible that everything is mere chance, though one who has studied plant teratology is astounded at the almost infinite number of characters that have appeared that were absolutely dangerous to the individual in its contest for survival. Be that as it may, I simply wish to acknowledge unbelief in any so-called proof that the inheritance of acquired characters is *impossible.* At the same time one must admit that no unquestionable proof of such inheritance has ever been submitted. Experimental evidence is woefully negative. It seems only reasonable, therefore, considering the available corroborative evidence, to relegate the expression of new characters to variations that have affected the potentialities of the germ cells. We can simply divide variations into the classes inherited and non-inherited without any admission as to their cause. We can call the inherited variations mutations if we will, or we can give them any other name. We must simply remember that they are both large and small.

One can hardly agree with Osborn that *large* variations which are not in an orthogenetic line have had little value in evolution, or that teratological phenomena are of little consequence. The production of identical quadruplets in the armadillo can scarcely be a gradually perfected character. Zygomorphism in flowers is lost as a unit and although this does not prove its birth as a unit, still that is to be presumed. One could fill pages with such data, but this is hardly the place for it. We will therefore consider the relative constancy of what we know as a unit character.

THE CONSTANCY OF UNIT FACTORS

The first thing one does if he wishes to oppose the idea of a unit character is to ask for a definition. A perfect definition of a unit character is as difficult to formulate as for a flower, yet one can obtain an idea of a flower by proper application. If one describes a unit character as the somatic expression of a single gametic factor or heredity unit, he at once gets into trouble. As the factor and not the character is the descriptive unit, a unit factor may affect a character but that character may never be expressed except when several units cooperate in ontogeny. I should prefer to disregard the word character therefore in formulating the problem. The real problem is: Are the facts of heredity adequately described by unvarying hypothetical factors? It is my thesis that if they can not be so described, the Mendelian notation fails.

Johannsen was the first to show the relative constancy of characters by his beautiful experiments on beans. Since that time, experiments designed to show change, if present, have yielded negative results on bisexual animals such as poultry (Pearl), on plants such as peas (Love), beans (Johannsen's later work), maize (Shull, East, Emerson), on asexual animals such as hydra (Hanel), paramæcium (Jennings) and on asexual plants such as bacteria (Barber and others), and potatoes (East).

Three critics have appeared. Karl Pearson took up the gage of battle because Johannsen's work shows the utter untenability of the correlation coefficient as a measure of heredity. He has produced no evidence to uphold his view. Harris, following Pearson for a like reason, has concluded against Johannsen, but has not yet presented his data for public criticism. There remains the work of Castle, which he believes is supported by the work of Woltereck. The question to consider then is whether the work of these two investigators justifies the contention.

Castle states that by selection he has modified a unit character. No one questions that under certain conditions changes in characters are made manifest by selection. It has been done again and again. The question as I see it is the following: Are not the facts presented by Castle and the facts of the pure-line workers described most concisely and in a way most helpful to investigation, by the reactions of fixed and unchanging units? If they can not be thus described the use of units is an absurdity, for one can not measure or describe by changing standards.

Castle's principal work on selection is with a fluctuating black and white coat pattern—the so-called hooded rat. In writing of these experiments, Castle says (*l. c.*, p. 355):

> I shall speak first of the case least open to objection from the genotype point of view, which requires:
>
> 1. That no cross breeding shall attend or shortly precede the selection experiment, lest modifying units may unconsciously have been introduced, and
>
> 2. That only a single unit-character shall be involved in the experiment.
>
> These requirements are met by a variety of hooded rat which shows a particular black and white coat pattern. This pattern has been found to behave as a simple Mendelian unit-character alternative to the self-condition of all black or of wild gray rats, by the independent investigations of Doncaster, MacCurdy and myself. The pigmentation however in the most carefully selected race fluctuates in extent precisely as it does in Holstein or in Dutch Belted cattle. Selection has now been made by Dr. John C. Phillips and myself through 12 successive generations without a single out-cross. In one series selection has been made for an increase in the extent of the pigmented areas; in the other series the attempt has been made to decrease the pigmented areas. The result is that the average pigmentation in one series has steadily increased, in the other it has steadily decreased. The details of the experiment can not be here presented, but it may be pointed out (1) that with each selection the amount of regression has grown less, *i. e.,* the effects of selection have become more permanent; (2) that advance in the upper limit of variation has been attended by a like recession of the lower limit; the total range of variation has therefore not been materially affected, but a progressive change has been made in the mode about which variation takes place.
>
> 3. The plus and minus series have from time to time been crossed with the same wild race. Each behaves as a simple recessive unit giving a 3:1 ratio among the grandchildren. But the extracted plus and the extracted minus individuals are different; the former are the more extensively pigmented.
>
> 4. The series of animals studied is large enough to have significance. It includes more than 10,000 individuals.
>
> The conclusion seems to me unavoidable that in this case selection has modified steadily and permanently a character unmistakably behaving as a simple Mendelian unit.

This conclusion, from the writer's standpoint, is not only avoidable, but unnecessary. No direct or implied denial of these facts is made, but a shift is made in the point of view. It seems to me a logical necessity that hypothetical units used as measurement or descriptive standards be fixed. The problem to be solved is the simplest means of thus expressing the facts. If the most definite characters—*i. e.,* certain pure-line homozygotes—are sufficiently constant in successive generations to be expressed by a fixed standard, well and good. The whole heredity shorthand is then simple. If such is not the case, the *character* must still be described by some fixed standard, but in that case recourse must be had to complex mathematical expressions and not to a single unit to describe the most constant somatic expressions. Furthermore, if these mathematical expressions served any practical purpose, it would be necessary to prove that all somatic variability of homozygotes under uniform conditions (if there is any) may be expressed by very few formulas.

Such an attitude does not seem to be in harmony with the progressive spirit of the times. I believe that we may describe our results simply and accurately by holding that unit factors produce identical ontogenetic expressions under identical or similar conditions. If under identical conditions the expression *is* different, then a new standard, a new unit, must be assumed; that is, factor *A* by any change becomes factor *B*. The results of the pure-line investigations are the warrant for this interpretation, for they are the investigations of successsive generations of somatic expressions with the least attendant complication. From them one may assume that a succession of individuals homozygous in all characters and kept under identical conditions will be alike.[4] To be sure there are numerous changes in the expression of characters when external and internal conditions are not so uniform as the above, but I believe that these changes can all be described adequately and simply by ascribing them to modifying conditions both external and internal. When external we recognize their usual effect in what we called non-inherited fluctuations, when internal we recognize their cause in other gametic factors inherited independently of the primary factor but modifying its reaction during development. This is a physiological conception of heredity, as it recognizes the great coöperation between factors during development. It is a very simple conception of heredity, moreover, for it allows a multitude of individual transmissible differences with the assumption of a very few factors. Some illustrations will be given later that will show the idea underlying this theory. Let us now see whether Castle's work can be described properly by it.

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[4] Possibly even under these conditions rare variations that are exceptions to this rule might occur. In other words, mutations might occur having no external cause and therefore to be left for vitalistic interpretation, but this would not affect the general situation.

Castle started with a peculiar character. It fluctuates continually and has never been bred to as small a variability as have many other characters. I have worked with a somewhat similar character in maize. It is a variegated pericarp color. In experimenting with it I have raised over a thousand progeny in one generation, a thing manifestly impossible with rats. Both solid colored ears and white ears have been obtained, and while at present it would be unwise to draw definite conclusions, it appears that both solid red ears and white ears of this kind give again variegated progeny. In other words, neither the red ear nor the white can behave like a normal red or white ear, but as if the pattern had fluctuated so widely that it can not appear on the ear (this explanation was suggested by Emerson). At any rate, we may conclude that the rat pattern fluctuates widely and is therefore markedly affected by some condition either internal or external.

Castle began therefore with a character in a fluctuating condition, possessed by a race which had not recently been crossed with a different race. This does not mean, however, that the various individuals forming his original stock did not differ in several factors that in their different combinations might have an effect upon the developing pattern. Suppose for the moment that this were actually the case. If he had been able to produce a fraternity by a single mating numbering several thousands, he would have produced individuals with all of these combinations of other genes. It is probable that he would then have obtained his progressive extremes in one generation, extremes that were never seen when but few individuals were produced. This sort of a thing is not hypothetical. It is mathematically demonstrable that with the same variability $(a + b)^n$ expanded gives an increase in the number of classes as the total number of individuals increases. It is, moreover, supported by the experimental evidence of De Vries on selecting for higher number of rows in maize. I, myself, by using greater numbers obtained an increase in protein in maize in one generation comparable to that obtained by the Illinois Agricultural Station in three generations.

Castle further argues that decrease in regression toward the original mean supports his view. On the other hand, this is exactly what should take place on assuming the truth of the fixed factor conception, as has been shown by Jennings.

Again, the selected races when crossed with wild races both act as simple recessives, but the extracted plus individuals are more pigmented. This is what I should expect. The extracted plus individuals would be more pigmented when existing in small numbers, because the modifying factors are several. If several thousand progeny were grown, however, recombinations would show a more varied result. And as a matter of fact, extracted recessives from the plus race are not precisely comparable in their fluctuation to the selected race with which the wild was crossed. They are more variable than the progeny of an inbred hooded individual of the same grade as the parent used in the cross with the wild. I do not think that one has a right to say, therefore, that there were no modifying genes present in various combinations in the extracted recessives.

When the selected lines were crossed together, moreover, the resulting progeny were somewhat intermediate and variable. The grandchildren were *more* variable. This is what should result from our assumptions. The animals are homozygous as far as having a pattern is concerned, but they differ in several genes that affect the development of the pattern.

Taking into consideration all the facts, no one can deny that they are well described by terminology which requires hypothetical descriptive segregating units as represented by the term factors. What then is the object of having the units vary at will? There is then no value to the unit, the unit itself being only an assumption. It is the expressed character that is seen to vary; and if one can describe these facts by the use of hypothetical units theoretically fixed but influenced by environment and by other units, simplicity of description is gained. If, however, one creates a hypothetical unit by which to describe phenomena and this unit varies, he really has no basis for description.

The facts obtained when working with pied types are complex. They are evidently not thoroughly understood as is evidenced by a different interpretation made by every worker who has investigated them. Doncaster and Mudge see two types of Irish rat. Why not three or four? Crampe obtained hooded rats from cross of self-colored and albino, the hooded coming only from heterozygotes having some white. No adequate explanation has been given. Cuénot concluded regarding pied mice with several degrees of piedness that each was recessive to the other of next higher grade. In fact the behavior of self colors and spotted colors among mammals as among plants is pretty well ''confused,'' as in several species spotted types dominant to self color are known.

Castle's other experiments in selection—the formation of a four-toed race of guinea-pigs starting with one animal with a rudimentary fourth toe, and the perfection of a silvered race of guinea-pigs from an animal in which the character was feebly expressed—need not be considered here. Both were necessarily crossed with normals at the start, and gradual isolation of races having the proper gene complex for complete expression of the characters is to be expected. There have been numerous selection experiments of this type—such as those of De Vries, the Vilmorins, the Illinois Agricultural Experiment Station, etc.—that have yielded results.

But these results, with one possible exception, were open to the criticism that they probably had to do with mixed lines and could therefore be described by the notation we have used. The experiments on pure lines have given no such results. One should not be asked to accept the results of the unguarded experiments and disregard the results of the guarded investigations.

The one possible exception alluded to above refers to the experiments of Woltereck (*Deut. Zool. Gesell.,* 19: 110–173, 1909) on parthenogenetic strains of *Hyalodaphnia* and *Daphnia* where there can be no question of gametic recombination. This experiment is not beyond criticism as will be seen later, but if it were our position would not be affected. The results would still have to be described by some *fixed standard* but the description would be complicated. *Since it is not beyond criticism, there is yet no reason for such a complication.*

Woltereck's work was primarily to show whether or not acquired characters are inherited. It was a secondary object to find out whether small variations or distinct sports occurred in the species. Those who use the work as an argument for unit factor modification, therefore, should also accept his inheritance of characters acquired.

Woltereck tested the effect of selection on seven characters. Selection gave *no* results in five cases. The first supposedly successful case is for difference in head height. In different pure lines he found an enormous effect of environment. He therefore endeavored to plot curves for different kinds of environment, food, temperature, generation number, etc. By comparing these curves he makes an argument for the inheritance of small acquired variations. In the absence of control cultures, and from the fact that culture conditions very uniform to Dr. Woltereck may have been somewhat extreme to Mr. A. Daphnia, the argument has only the value of the other numerous scholastic defences of inherited acquirements. It is criticized by Tower in a recent publication. Woltereck did obtain one inherited head variation. It apparently arose suddenly. He calls it a mutation.

The only result that can be considered seriously from the standpoint taken in this paper is the result when selecting for a rudimentary eye. *Daphnia* has been distinguished from *Hyalodaphnia* by the presence of a rudimentary eye. The distinction does not seem to be valid, for Woltereck noticed rudimentary eyes several times in pure line cultures of *Hyalodaphnia* and they have also been seen by others in wild cultures. He regards the phenomenon as a reversion to a preexisting condition. *He found that the presence of the rudimentary eye is periodic. In the spring it appears, in the summer it again disappears.* Either kind can produce progeny of the other kind. From this fact it seems reasonable to believe that environment or generation number has much to do with the expression of the character, although Woltereck in one place inclines to the opinion that external factors affect it but little. He performed several experiments on the effect of light and temperature, however, and says that provisionally they gave no result free from objection—" . . . gegaben einstweilen kein einwandfreies Resultat." Almost any interpretation can be given this statement.

From a pure line in which this variable eye spot appeared, he isolated a mother and grandmother with the character well developed. Ninety per cent. of the progeny had the eye well developed. The rapidity of his results and the fact of *periodicity* in the expression of the character makes any cumulative effect of selection exceedingly questionable. One is not justified therefore in accepting it as proof without corroboration.

CONCLUSION

In conclusion, it may be asked if it is not reasonable to accept simply as a nomenclature the description of the whole facts of inheritance in sexual reproduction given by the Mendelian system? Is it wise to turn backward and to give up this handy and helpful notation right in the midst of a useful career? The experiments least open to objection (the pure-line experiments) have shown the wisdom of assuming a stable unit factor, this factor being representative of the stability manifested by a character complex when no interfering conditions intervene. Let us accept this simple interpretation provisionally, appreciating the fact that the stability of the characters that have been represented by fixed units may be only a static appearance due to limited experiments; but that this appearance justifies our neglecting any infinitesimal fluency of our factor standards in experiments of like duration, since taking them into account would necessitate a change of standard, a new fabric of hypotheses and a more complicated system. Let us take a physiological view of heredity. Factors are assumed to be stable. Characters are somewhat unstable owing to the effect that other factors have upon their expression. Factor *A*, for example, is potentially able to produce a typical expression in ontogeny under certain definite conditions of environment, but the presence or absence of *B* or *C* or *D* or *B*, *C*, and *D* are responsible for slight changes in the expression of *A*. This conception gives us a picture of heredity in real accordance with physiological facts, in contradistinction to the non-biological and fixed physical conception—the mosaic organism conception—that critics often say is held by some geneticists.

One may answer that this conception is all right for quantitative characters, but do the facts uphold it for qualitative characters? They do. I will give examples from my own experiments on the inheritance of the purple aleurone cells in maize. Here one obtains progeny by the thousands and sees phenomena that are obscured by lesser numbers.

Crosses of the purple variety with three different whites have given three different results. One shows that the purple may be represented by the schematic description *PPRRCC*. Crossed with *pp rr cc* it gives purples, reds and whites in the F_2 generation, as all three factors are necessary for the production of the purple color. How many other factors (present also in the whites) may be necessary one can not say. In another white, the *R* factor is present and purples and whites in the ratio of 9:7 result. In another white, both *P* and *R* are present. In another white, both *P* and *C* are present. Both give monohybrid ratios when crossed with the purple.

This is not the sum total of whites, however; several others have been found. One has an intensifying factor. We get darker purples together with the normal purples, but no one can doubt that the purple is still the same pigment modified in its expression. Another white has a dominant inhibiting factor. In the heterozygous condition it does not always inhibit the color entirely, but in the homozygous condition color never develops. The dominance of this factor is proved by the fact that extracted colored recessives are still heterozygous for presence of color.

In still other whites I have demonstrated the presence of at least three modifying genes $M_1M_2M_3$. They are independent of each other, yet each and all affect the purple color. One is dominant, as if it were a partial inhibitor, the others are recessive, as if they were the loss of intensifying factors. Purples of all different degrees can be isolated and breed true. The lightest is such that the color can be distinguished only with a lens. But they are all strictly alternative in their transmission and somewhere near the expected ratios of darks, lights, very lights, etc., appear. It is too much to ask that exact ratios be obtained for with this kind of modification all shades appear, yet conclusive evidence has been obtained by F_3 and F_4 generations.

The qualitative characters do act the same as quantitative characters, therefore, and one can not make a real distinction between them.